

Population dynamics and habitat use of cervids in southern Argentine Mesopotamia

Julian Alberto Sabattini

`julian.sabattini@uner.edu.ar`

National University of Entre Ríos

Norberto Muzzachiodi

National University of the Littoral

Mariano Lisandro Merino

National University of Northwestern Buenos Aires

Ivan Alberto Sabattini

Natural Protected Area La Esmeralda

Research Article

Keywords: Axis axis, Subulo gouazoubira, population density, camera traps

Posted Date: June 2nd, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-9837383/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Discover Life on October 12th, 2026. See the published version at <https://doi.org/10.1007/s11084-026-09769-x>.

Population dynamics and habitat use of cervids in southern Argentine Mesopotamia

Sabattini J.A.¹, Muzzachiodi, N.², Merino, M. L.³, Sabattini I. A. ⁴

1. Ecología de los Sistemas Agropecuarios, Facultad de Ciencias Agropecuarias, Universidad Nacional de Entre Ríos-CONICET. Dasonomía, Facultad de Ciencias Agrarias, Universidad de Concepción del Uruguay. Entre Ríos, Argentina
2. Cátedra Gestión Ambiental. Universidad Nacional del Litoral. Facultad de Bioquímica y Ciencias Biológicas. 3000. Santa Fe, Argentina.
3. Comisión de Investigaciones Científicas de la Provincia de Buenos Aires. Universidad Nacional del Noroeste de la Provincia de Buenos Aires (UNNOBA). Buenos Aires, Argentina.
4. Profesional independiente, Área Natural Protegida, Establecimiento La Esmeralda. Entre Ríos, Argentina.

Corresponding author: Julian Alberto Sabattini, E-mail: julian.sabattini@uner.edu.ar

Abstract

Cervids constitute one of the most representative mammalian groups inhabiting the natural environments of the Argentine Mesopotamia; however, ecological information regarding their population patterns within productive systems associated with natural habitats remains limited. The aim of this study was to analyze the relative abundance, activity patterns, and temporal overlap between the exotic *Axis axis* and the native *Subulo gouazoubira* in two characteristic natural environments of southern Argentine Mesopotamia: native forest and riparian forest. The study was conducted in the Protected Natural Area “La Esmeralda” (Entre Ríos, Argentina) using camera traps deployed between July 2022 and January 2024. Relative abundance indices, circadian activity patterns through Kernel Density and STN analyses, temporal overlap coefficients, and population density estimations were calculated. *Axis axis* exhibited higher relative abundances in both environments, particularly within riparian forests, demonstrating high ecological and temporal plasticity. In contrast, *Subulo gouazoubira* showed lower abundances and predominantly crepuscular activity associated with environments characterized by greater vegetation cover. Both species were classified as cathemeral; however, continuous analyses revealed important functional differences, with axis deer displaying more flexible and extended activity patterns. Temporal overlap was high in both environments, although more variable within native forests. These findings provide relevant ecological information for understanding the coexistence of native and exotic cervids within the natural environments of the Argentine Espinal.

Keywords: *Axis axis*, *Subulo gouazoubira*, population density, camera traps.

Introduction

Entre Ríos is a distinctive province within the Argentine Mesopotamia due to its undulating topography, which gives rise to highly heterogeneous environments. Both its native flora and fauna are strongly influenced by the diversity of interacting ecological factors (Muzzachiodi and Sabattini, 2021; Rojido et al., 2022; Barzan et al., 2023). In particular, native forest ecosystems have undergone extensive transformation during recent decades as a consequence of increasing deforestation processes (Jozami and Muñoz, 1982; Muñoz et al., 2005; Maldonado et al., 2012; Sabattini et al., 2015; Avogadro and Padró-García, 2019). Nevertheless, recent studies reported that forest cover still represents 26.4% of the provincial territory (more than 2 million ha), whereas natural grasslands, another representative ecosystem, account for more than 34.1% of the province (Sabattini et al., 2024). Consequently, over 60% of the provincial territory remains covered by highly valuable natural ecosystems, not only for sustainable agricultural production, but also for providing habitat to native and exotic wildlife species, particularly cervids.

The most conspicuous cervids in the region are *Axis axis* (Erxleben, 1777) and *Subulo gouazoubira* (Fischer, 1814). These syntopic species share their distribution across much of central and northeastern Argentina, including the Espinal, Campos y Malezales, Paraná Delta,

and Iberá Wetlands ecoregions (Calfayan, 2021). *Axis axis*, an exotic species originating from the Indian subcontinent, is considered a habitat generalist (Tellarini et al., 2023). However, it shows preference for forest–grassland mosaics with moderate tree cover due to its dependence on permanent water availability and abundant graminoid resources throughout the year (Tellarini et al., 2019). The species was introduced during the early twentieth century in Buenos Aires Province (Navas, 1987) and subsequently expanded throughout much of Argentina, particularly within the Mesopotamian region. It is recognized as a highly invasive species capable of reaching elevated population densities, thereby generating significant impacts on native vegetation communities (Tellarini et al., 2023).

Conversely, the brown brocket deer (*Subulo gouazoubira*) is a native cervid of smaller body size (Muzzachiodi et al., 2022), capable of occupying environments similar to those used by *Axis axis*, including forest edges and shelterbelts (Paviolo et al., 2009; Juliá et al., 2019), highly fragmented forest landscapes (Berduc, 2002), and forested areas associated with grasslands or croplands (Muzzachiodi et al., 2022). This supports the hypothesis that ungulates with smaller home ranges predominantly use more closed habitats (Ofstad et al., 2016). Some studies suggest that the exotic deer may be displacing the brown brocket deer through habitat competition, thereby restricting its distribution (Juliá et al., 2019). Nevertheless, hunters, park rangers, and landowners have reported observing mixed groups composed of both cervid species (Muzzachiodi et al., 2022), reinforcing their condition as syntopic species, that is, species capable of coexisting within the same habitat, simultaneously occupying the same physical space while sharing highly similar environmental conditions and resources (Pianka, 1974, 2000; Begon et al., 1986).

This situation raises important concerns regarding the ecological impacts generated by exotic species invasions, including population changes in ecologically similar faunal groups, significant biodiversity losses at multiple spatial scales, and alterations in ecosystem functioning and ecosystem service provision (Bohan et al., 2017; Brondizio et al., 2019; Vantarová et al., 2023; Valenzuela et al., 2023). These knowledge gaps concerning cervids have been highlighted in regional studies (Eberhardt et al., 2009; Relva and Sanguinetti, 2016; Solís Neffa et al., 2021; Suarez Castro et al., 2021; Gürtler et al., 2024), particularly because they seek to determine the actual effects of exotic species on native fauna displacement, especially under scenarios involving interactions with domestic livestock (Rebollo and Gómez, 2003; Botero and De La Ossa, 2011; APN, 2019; Di Bitetti et al., 2020; Jori et al., 2021; Arias and Guzmán, 2023). Effective wildlife conservation and management largely depend on the availability of information regarding fundamental population parameters and species behavioral ecology (Monroy-Vilchis et al., 2011). In this context, low-cost methodologies such as camera trapping provide highly valuable ecological information.

Camera traps are widely used tools in wildlife population studies (Karanth, 1995; Fedriani et al., 2000; O'Connell et al., 2006; Lizcano, 2018; Palencia et al., 2021), as they enable long-term, non-invasive data collection (Carthew and Slater, 1991; Trollet et al., 2014). These methodologies allow the assessment of population dynamics, behavioral patterns, and interspecific spatiotemporal relationships, among other ecological parameters (Nichols et al., 2011). Consequently, ungulates have been extensively studied using camera-trap approaches (Periago, 2006; Pérez-Irineo and Santos-Moreno, 2016; Vila et al., 2016; Grax et al., 2018; Nakashima et al., 2020). Population density represents another key parameter estimated through camera-trap methodologies, both for wildlife conservation and management purposes (Henrich et al., 2022; Palencia et al., 2022), as well as in contexts where wildlife interacts with productive systems. Based on camera-trap capture data, numerous density estimation models have been developed (Chandler and Royle, 2013; Gilbert et al., 2021; Hayashi and Iijima, 2022; Li et al., 2022; Lyet et al., 2024; Palencia et al., 2023; Zampetti et al., 2024). Among these, the REST model (Random

Encounter and Staying Time; Hongo et al., 2021; Nakashima et al., 2020, 2025, 2026) estimates population density using encounter rates and the time individuals remain within the camera detection area.

Given the limited ecological information available for cervids in the region, and using photographic records obtained through camera traps, the objectives of this study were: (a) to characterize the activity patterns of the cervid species present (brown brocket deer and axis deer), and (b) to estimate their population density in two representative native forest environments located in southern Argentine Mesopotamia.

Material and Methods

Study area

The study was conducted in the Protected Natural Area (PNA) “La Esmeralda” (hereafter, PNA “La Esmeralda”), located in the central-northern region of Entre Ríos Province, Argentina (-31.393001 S, -59.708379 W) (Figure 1). The region is characterized by a humid temperate plain climate without a dry season, where annual precipitation gradually decreases from northeast to southwest, ranging from approximately 1,400 to 1,000 mm per year. Rainfall is mainly concentrated during spring and summer; however, both annual precipitation and its seasonal distribution have changed during recent decades as a consequence of global climate change (Sabattini and Sabattini, 2021). Mean annual temperature ranges between 16 and 20 °C, decreasing progressively with increasing latitude (Sasal et al., 2019). The landscape is characterized by undulating topography, which strongly influences soil distribution and generates marked physiognomic, structural, and floristic heterogeneity in the vegetation (Sabattini et al., 1999). The native vegetation belongs to the Espinal Phytogeographic Province (Oyarzabal et al., 2018), floristically dominated by *Neltuma nigra* Griseb., *N. affinis* Spreng., and *Vachellia caven* Molina. Medium and upper topographic positions are dominated by tall native forests with abundant shrub vegetation, whereas riparian forests develop along stream margins, characterized by greater arboreal cover, a well-developed shrub layer, and sparse herbaceous vegetation (Sabattini et al., 2015). From a productive perspective, cultivable lands are mainly used for extensive agriculture, including cereal crops such as wheat and maize, as well as oilseed crops such as soybean and flax, whereas cattle production is commonly associated with natural environments (Sabattini et al., 2024).

Experimental design

Camera traps were used to characterize activity patterns, estimate population density, and evaluate potential interactions between *Subulo gouazoubira* (brown brocket deer) and *Axis axis* (axis deer) in the presence of cattle and horses. Camera trapping is a widely used methodology for determining species occurrence, daily activity rhythms, and temporal overlap among species, among other ecological parameters (Monroy-Vilchis et al., 2011; O’Connell et al., 2011; Muzzachiodi et al., 2020; Muzzachiodi and Sabattini, 2025). From July 2022 to January 2024, monitoring was conducted using four camera traps: two installed in semixerophytic native forest environments (TC3: -31.3900, -59.7181 and TC4: -31.3896, -59.7180), and two located within riparian forests (TC1: -31.3919, -59.7181 and TC2: -31.3846, -59.7079).

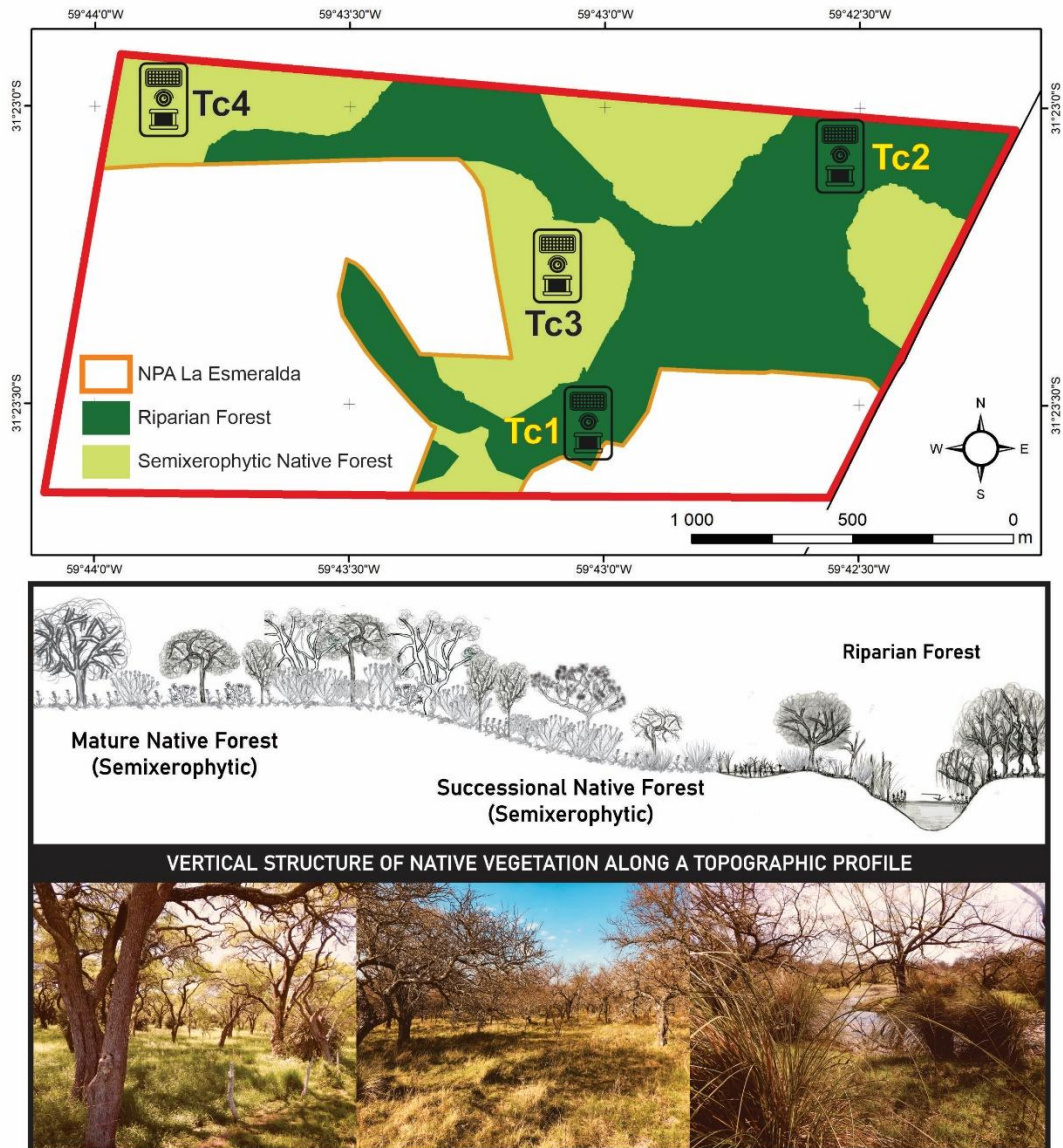


Figure 1. Geographic location of the camera-trap stations and vertical profile of native vegetation along a topographic gradient within the PNA “La Esmeralda”.

Operationally, the experiment lasted 554 days, with up to 1,174 capture events recorded by the most effective camera station. Camera traps were configured to capture three consecutive photographs followed by a 10-second video, with a 15-second delay interval between events. Watermark metadata, including camera identification, date, time, and other default information, remained activated throughout the monitoring period. No bait or attractants were used to increase animal detection probability. Data were retrieved every 20 days, and each image was manually identified to construct a database containing all recorded species, corresponding date, time, taxonomic identification, and ambient temperature. Camera traps were mounted on trees at a height of approximately 30–40 cm above ground level.

Relative abundance estimation

The Relative Abundance Index (RAI) has become a widely used metric for estimating species abundance from photographic records obtained through camera traps. Its principal advantage lies in the simplicity of its calculation and its ability to compare the relative contribution of each species within a community while simultaneously reducing sampling effort. Nevertheless, this

approach is not free from limitations, since the relationship between relative abundance and actual population density may vary among habitats or over time, and biases associated with imperfect detection probabilities may compromise estimation accuracy (O'Brien, 2011; McIntyre et al., 2020).

In general, the RAI reflects the relative frequency with which species are recorded within the dataset and, although it constitutes an indirect measure of abundance, it is often positively correlated with population density (Nichols, 1992; Karanth and Nichols, 2002). The classical index, based on the number of independent photographic records per camera-trap day, has been the most commonly applied approach (O'Brien, 2011; Mandujano, 2019). However, when the objective is to preserve the spatial information associated with each camera station and compare environments with different sampling efforts, alternative estimators such as those proposed by Mandujano (2019) are more appropriate, considering an independent RAI calculation for each camera:

$$RAI_{ij} = \frac{n_{ij}}{d_j} \times 100$$

where n_{ij} corresponds to the number of records of species i at camera j , and d_j represents the number of operational days for that camera station. This formulation allows the calculation of means and measures of variation (standard deviation or standard error), thereby facilitating statistical comparisons among species and environments. In addition to preserving the spatial variability of the dataset, this approach provides dispersion estimates, which are essential for robust statistical comparisons between species and habitat types.

Activity patterns and overlap analysis

For activity pattern analyses, no independence criterion among records was applied, since eliminating autocorrelation may limit and bias the results by failing to reflect the continuous nature of animal activity (De Solla et al., 1999; Blundell et al., 2001; Peral et al., 2022). Instead, all available records were included, maximizing estimation accuracy in the analyses of activity patterns. Species were classified according to their daily activity cycles (circadian rhythms) as follows: species with $\geq 70\%$ of their records between 08:00 and 16:59 h were classified as diurnal; those with $\geq 70\%$ of records between 21:00 and 03:59 h were considered nocturnal; and species with $\geq 70\%$ of records within the intervals 04:00–07:59 h and 17:00–20:59 h were classified as crepuscular. Species that did not satisfy these criteria, exhibiting activity during daytime, nighttime, and crepuscular periods, were classified as cathemeral. Additionally, combined categories (diurnal/crepuscular and nocturnal/crepuscular) were defined when 90% of the records were distributed across both temporal intervals (Albanesi et al., 2016).

Daily activity patterns were estimated in the R environment (R Core Team, 2013) using the package *Overlap* (Ridout and Linkie, 2009; Linkie and Ridout, 2011; Lynam et al., 2013; Pastore, 2018; Meredith and Ridout, 2020). In this procedure, the probability density function of activity records was estimated non-parametrically using Kernel Density Estimation (KDE) and the Non-negative Trigonometric Sum (STN) distribution function. These approaches treat each record as a random sample drawn from an underlying continuous activity distribution (Fernández-Durán, 2004; Ridout and Linkie, 2009), thereby avoiding the bias associated with grouping observations into arbitrary temporal intervals (Pratas-Santiago et al., 2016).

Temporal niche overlap between species pairs was estimated from species-specific probability density functions ($f(x)$ and $g(x)$) using the overlap coefficient Δ (Ridout and Linkie, 2009; Linkie and Ridout, 2011). This index ranges from 0 (no overlap) to 1 (complete overlap). Confidence intervals (95%) were estimated using 1,000 smoothed bootstrap replicates derived from the

estimated density distributions (Meredith and Ridout, 2018). To avoid biases associated with sample size, estimator $\Delta 1$ was used for small samples (<50 records), whereas $\Delta 4$ was applied to large samples (≥ 50 records) (Ridout and Linkie, 2009). Finally, overlap levels were interpreted following Monterroso et al. (2014) as low ($\Delta \leq 0.5$), moderate ($0.5 < \Delta \leq 0.75$), and high ($\Delta > 0.75$). Simulations were performed at both seasonal and annual scales, within and between both cervid species (brown brocket deer and axis deer).

Population density estimation

Population density was estimated using the REST model (Random Encounter and Staying Time; Nakashima et al., 2021), which combines encounter rates with the residence time of individuals in front of camera traps. The effective detection zone was defined according to the field of view and sensor range of each camera-trap unit. Data processing followed standardized criteria to ensure record independence. To reduce potential biases, all events were considered independent in order to avoid pseudoreplication (Tobler et al., 2008, 2009). Consequently, all photographs of the same species obtained at the same sampling station within a one-hour interval were considered a single independent record. In the case of gregarious species, each observed individual was treated as an independent record (Pérez-Irineo and Santos-Moreno, 2016). Based on these independent events, a presence–absence dataset was generated for each species at each camera station according to sampling days (Gallina and López-González, 2011). For each event, two fundamental parameters were extracted: the number of encounters per unit of time and the average residence time of individuals within the detection area. Density analysis was based on the relationship among encounter rate (γ), residence time (t), and the effective detection area of the camera (A). In its basic form, population density (D) was estimated as

$$D = \frac{\gamma}{t \times A}$$

where (γ) corresponds to the encounter rate per station and per unit of time, (t) represents the mean residence time of individuals within the camera field of view, and (A) corresponds to the effective area covered by the camera trap. Density estimates were obtained using maximum likelihood procedures, complemented by Bayesian approaches to incorporate uncertainty. In some cases, environmental covariates were also integrated into the models to explain spatial variation in density and residence time.

The REST model relies on several assumptions that must be satisfied to ensure the validity of the estimates: (1) the population is assumed to remain closed throughout the study period, such that no significant changes occur due to migration, natality, or mortality; (2) sampling stations are distributed randomly or systematically, avoiding concentrations in predictable movement corridors that could bias encounter rates; (3) animals do not modify their behavior in response to the presence of camera traps; (4) all individuals entering the detection area are recorded by the device; and (5) defined events satisfy the independence assumptions required for statistical analyses.

The application of the REST model allows the estimation of absolute population densities for species that cannot be individually identified, representing an important advantage over traditional methods such as Capture–Recapture approaches. Furthermore, this methodology enables comparisons of density among different habitat types, evaluation of environmental drivers influencing wildlife populations, and assessment of anthropogenic impacts on wild fauna. These results are particularly relevant for the development of wildlife management and

conservation strategies, monitoring of threatened species, and decision-making processes related to ecosystem restoration and sustainable land-use practices.

Results

Relative abundance estimation

The analysis of Relative Abundance Indices (RAI) revealed marked differences among sites and species. *Axis axis* exhibited the highest values at riparian forest site CT2 (RAI = 91.89; 442 events), followed by CT4 within the native forest (RAI = 69.47; 289 events), whereas intermediate and lower values were recorded at CT1 and CT3, respectively. These results suggest that axis deer maintain high occurrence frequencies within riparian environments, while also successfully establishing in native forest sectors. In contrast, *Subulo gouazoubira* showed a stronger association with riparian habitats, with relatively high values at CT1 and CT2 (RAI = 35.02 and 41.16, respectively), and a marked reduction in native forest records, where values only reached RAI = 16.11 at CT4 and 5.99 at CT3.

The interspecific comparison revealed a differential distribution pattern between both cervids. Whereas the exotic axis deer exhibited remarkable ecological plasticity and the ability to occupy both riparian and native forest environments, the native brown brocket deer appeared more restricted to gallery forest habitats. This difference in habitat use may reflect processes of spatial segregation or even ecological displacement, whereby the expansion of axis deer reduces habitat availability for the brown brocket deer in more heterogeneous environments. The consistently greater abundance of the exotic species across all sites reinforces its condition as a successful invader, whereas the native brown brocket deer may be experiencing limitations associated with habitat availability and interspecific competition, with important implications for the conservation and management of native wildlife in the region. Overall, abundances of the exotic axis deer were substantially higher within riparian forests than within native forests. A preliminary result derived from photographic records indicated that *Axis axis* co-occurred frequently with breeding cattle within riparian forests, with repeated detections at the same sampling sites. In contrast, *Subulo gouazoubira* exhibited only occasional records associated with livestock presence, mainly during the spring of 2023. Within native forests, the presence of cattle did not prevent the detection of either *A. axis* or *S. gouazoubira*; however, in the latter species, a greater frequency of records was observed following livestock removal.

Activity patterns and temporal overlap

The analysis of activity patterns of *Subulo gouazoubira* in the two evaluated environments revealed notable differences in the intensity and temporal distribution of records throughout the daily cycle. Overall, the species exhibited a predominantly crepuscular behavior, with activity concentrated near dawn and, more markedly, at dusk (Figure 2). Within native forests, the density curve showed well-defined peaks, with a pronounced increase in activity between 17:00 and 20:00 h, coinciding with sunset, and a second, less intense peak near dawn. Activity during midday and early nighttime hours remained low, although not absent, reinforcing the tendency toward a primarily crepuscular activity pattern.

The distribution of records in this environment indicated that *S. gouazoubira* consistently uses transitional periods between daylight and darkness, corresponding to typical foraging and movement strategies described for the species. In contrast, within riparian forests the density curve was characterized by lower overall intensity and less pronounced activity peaks. Although increases in activity were also detected near dawn and dusk, these were less marked and accompanied by a relatively more diffuse activity pattern throughout the day. Consequently,

activity within riparian forests appeared more extended and less temporally concentrated than within native forests.

Direct comparisons between environments revealed that native forests sustained a higher frequency of records and more clearly defined density peaks, whereas records within riparian forests were less frequent and distributed with lower intensity. This difference was also reflected in the circular activity diagrams, which showed greater temporal concentration within native forests and a more dispersed activity pattern in riparian forests. These findings suggest that although *S. gouazoubira* maintained a crepuscular circadian pattern in both environments, its activity was more consistent, intense, and predictable within native forests, whereas in riparian forests the species exhibited a more diffuse activity pattern with lower relative frequency.

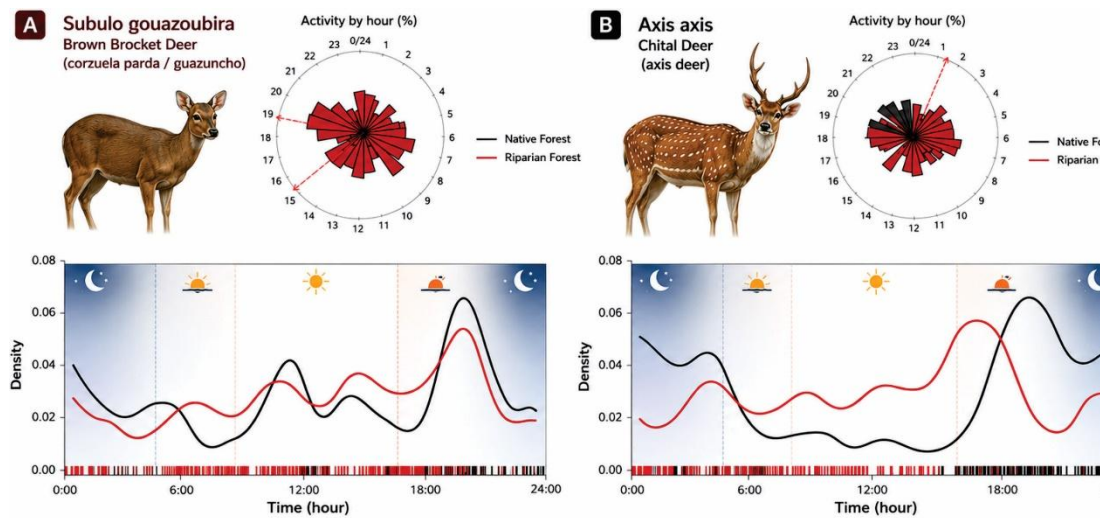


Figure 2. Daily activity patterns of *Subulo gouazoubira* (brown brocket deer) and *Axis axis* (chital deer) in native forest and riparian forest environments of the Argentine Espinal. Circular diagrams represent the relative frequency of activity records by hour, while continuous curves indicate probability density estimates derived from camera-trap data. Black lines correspond to native forest and red lines to riparian forest. Tick marks along the x-axis indicate the temporal distribution of independent photographic records.

The analysis of activity patterns of *Axis axis* revealed differences in both the intensity and temporal distribution of activity between riparian forests and native forests. Within native forests, the species exhibited a bimodal pattern, with a principal activity peak occurring around dusk (18:00–21:00 h) and a secondary increase during early nighttime hours (00:00–04:00 h). Diurnal activity remained relatively low and was restricted to periods close to midday (Figure 3). In contrast, within riparian forests the activity pattern was more diffuse and temporally extended, with relatively homogeneous records throughout the 24-hour cycle, although slight increases were still observed during dawn and dusk, albeit less pronounced than those recorded in native forests. Comparisons with *Subulo gouazoubira* demonstrated that, whereas the latter maintained a more restricted crepuscular pattern (well-defined peaks at dawn and dusk, particularly within native forests), *A. axis* exhibited a broader and more flexible behavioral pattern, combining nocturnal, crepuscular, and even diurnal activity, especially within riparian forests. This difference highlights a broader temporal niche utilization by the exotic species in contrast to the greater temporal specialization exhibited by the brown brocket deer.

The contrast between the methodological approaches applied to evaluate activity patterns revealed important nuances in the interpretation of the results. On one hand, the classification based on fixed temporal intervals (diurnal, crepuscular, and nocturnal) categorized both axis deer (*Axis axis*) and brown brocket deer (*Subulo gouazoubira*) as cathemeral across all sampling sites, since neither species concentrated $\geq 70\%$ of its records within a single period of the daily cycle (Figure 3). This methodology provides a practical and simplified description of activity patterns; however, it relies on arbitrary thresholds and the grouping of records into fixed temporal categories (Albanesi et al., 2016), potentially oversimplifying the complexity of circadian activity patterns.

In contrast, non-parametric probability density analyses (Kernel Density Estimation and STN) provided a more detailed and continuous representation of activity patterns, avoiding biases associated with arbitrary temporal grouping of the data (Ridout and Linkie, 2009; Pratas-Santiago et al., 2016). Under this analytical framework, *S. gouazoubira* exhibited a clearly crepuscular behavior, with well-defined peaks at dawn and dusk, whereas *A. axis* displayed a broader and more flexible activity pattern, characterized by extended activity during nocturnal and crepuscular periods. These results emphasize marked differences in the temporal strategies adopted by both cervid species.

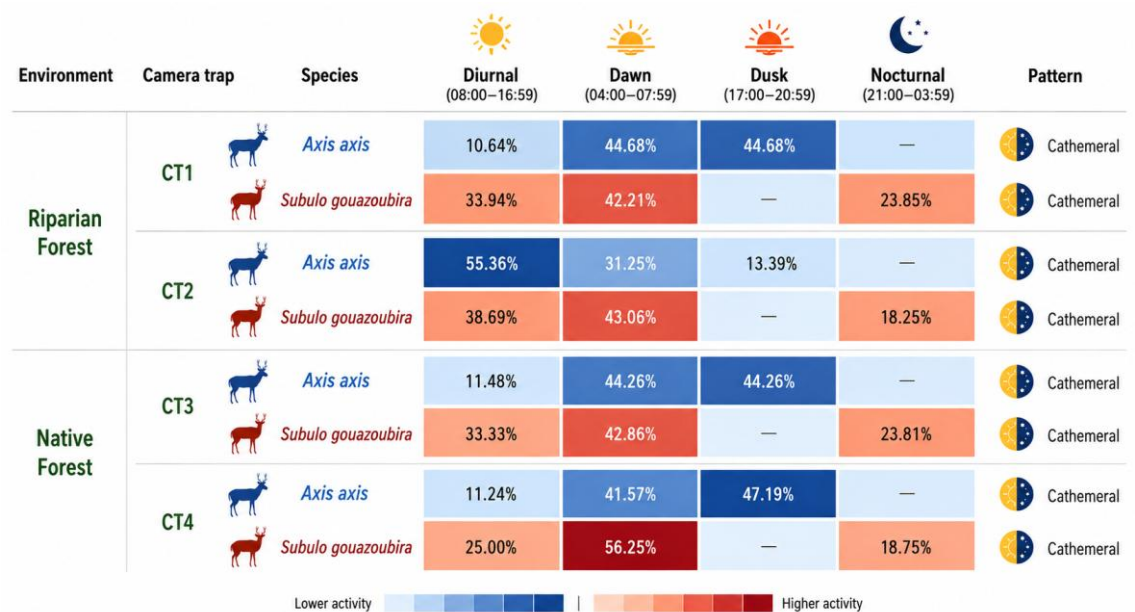


Figure 3. Relative distribution of daily activity patterns of *Axis axis* and *Subulo gouazoubira* across camera-trap stations in riparian forest and native forest environments. Percentages represent the proportion of activity records within four temporal intervals: diurnal (08:00–16:59 h), dawn (04:00–07:59 h), dusk (17:00–20:59 h), and nocturnal (21:00–03:59 h). Color intensity reflects relative activity levels within each temporal category. Both cervid species were classified as cathemeral across all sampling sites.

The analysis of daily activity patterns based on classification by temporal intervals indicated that both axis deer (*Axis axis*) and brown brocket deer (*Subulo gouazoubira*) exhibited a cathemeral pattern across all evaluated sites, meaning that both species remained active during daytime, nighttime, and crepuscular periods without concentrating more than 70% of their records within a single temporal interval. Nevertheless, differences in relative activity distribution were observed between species. *A. axis* displayed greater temporal flexibility, with a strong nocturnal

component at CT1, CT3, and CT4, and predominantly diurnal activity at CT2. In contrast, *S. gouazoubira* concentrated most of its activity during crepuscular periods, exhibiting a lower proportion of nocturnal records.

These findings complement the results obtained through probability density analyses, since although both cervids exhibited differential activity trends among environments (*A. axis* showing broader and more flexible activity patterns, and the brown brocket deer exhibiting stronger crepuscular tendencies), the overall classification under this methodological framework confirmed that both species should be considered cathemeral, reflecting their capacity to remain active throughout the entire 24-hour cycle.

These methodological differences should not be interpreted as contradictory, but rather as complementary approaches. Whereas interval-based classification confirms the cathemeral condition of both cervids—that is, their capacity to maintain activity throughout the entire daily cycle—probability density analyses allow the identification of relative temporal preferences and finer-scale overlap patterns, which are essential for understanding mechanisms of coexistence and potential competition between native and exotic species. In this context, the combined evidence suggests that although both species are cathemeral, the brown brocket deer remains more restricted to crepuscular periods, whereas axis deer exhibits greater temporal plasticity, potentially conferring competitive advantages within shared environments (Di Bitetti et al., 2008; Nanni, 2015; Di Bitetti et al., 2020).

Seasonal analyses of activity patterns of *Subulo gouazoubira* revealed variations in both the intensity and temporal distribution of activity between native forests and riparian forests (Figure 4).

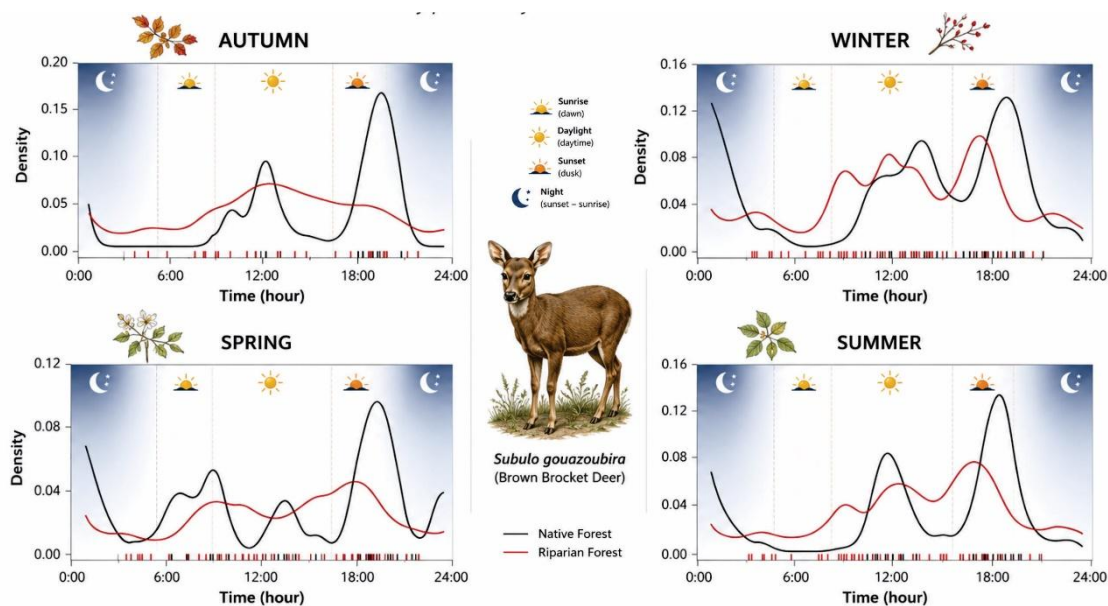


Figure 4. Seasonal activity patterns of *Subulo gouazoubira* in two environments: native forest (black line) and riparian forest (red line). Curves represent probability density estimates derived from camera-trap records for each season of the year (autumn, winter, spring, and summer). Lines located at the bottom of each panel indicate the temporal distribution of photographic records (red marks for riparian forest and black marks for native forest).

During autumn, the species exhibited a marked crepuscular-vespertine pattern within native forests, with a principal peak occurring at dusk (18:00 h) and a secondary increase around midday, whereas activity within riparian forests was lower and more diffuse, lacking clearly

defined peaks. During winter, activity increased in both environments, with native forests showing activity peaks during dusk and early nighttime hours, while in riparian forests activity was distributed more evenly throughout the day, with increases occurring both during morning hours and at dusk. In spring, the activity pattern within native forests was clearly bimodal, with peaks occurring at dawn and dusk, in contrast to riparian forests where activity remained low and temporally extended, with only a slight increase during the afternoon. Finally, during summer, activity patterns in both environments shifted toward a principal peak during the early morning hours (03:00–05:00 h) and a secondary peak at dusk (18:00 h), accompanied by reduced activity during midday, particularly within native forests, probably in response to elevated temperatures.

Overall, *S. gouazoubira* maintained a predominantly crepuscular pattern throughout the year, although important differences in activity intensity and temporal distribution were observed between environments. Native forests concentrated most activity during autumn, spring, and summer, whereas riparian forests exhibited a more diffuse and less intense pattern of habitat use, with the exception of winter, when greater overlap between environments was observed. *Axis axis* exhibited high temporal plasticity, with marked differences among environments and seasons (Figure 5).

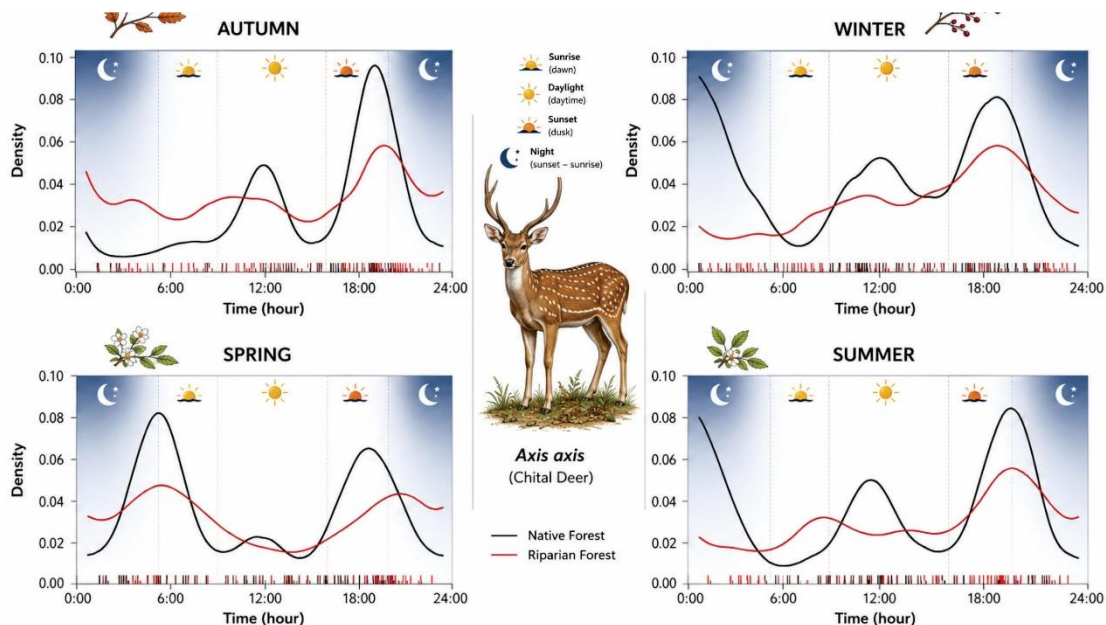


Figure 5. Seasonal activity patterns of *Axis axis* in two environments: native forest (black line) and riparian forest (red line). Curves represent probability density estimates derived from camera-trap records for each season of the year (autumn, winter, spring, and summer). Lines located at the bottom of each panel indicate the temporal distribution of photographic records (red marks for riparian forest and black marks for native forest).

During autumn, activity within native forests exhibited a bimodal pattern, with peaks occurring during early nighttime hours and at dusk, whereas within riparian forests activity was distributed more diffusely throughout the daily cycle, with increases during nighttime and early morning hours. During winter, axis deer intensified their nocturnal behavior within native forests, exhibiting pronounced peaks around midnight and during the early morning hours, accompanied by minimal diurnal activity. In contrast, within riparian forests, records were distributed more broadly, with activity progressively increasing from the afternoon toward nighttime hours. During spring, activity patterns within native forests became more fragmented, with multiple peaks occurring during early morning hours, midday, and dusk, whereas in riparian

forests a more clearly defined diurnal-crepuscular pattern predominated. Finally, during summer, *A. axis* exhibited several activity peaks within native forests (early morning, morning, and dusk), accompanied by reduced activity around midday, probably associated with elevated temperatures. In riparian forests, however, activity remained more homogeneous and sustained throughout the day, with slight increases during afternoon and nighttime periods.

Overall, *A. axis* exhibited a predominantly nocturnal-crepuscular activity pattern, although with marked seasonal and spatial plasticity. Activity was more temporally concentrated within native forests during autumn and winter, whereas broader and more diffuse activity patterns were observed in riparian forests and during warmer seasons.

Interspecific overlap analysis

The analysis of temporal overlap between *Axis axis* and *Subulo gouazoubira* revealed high overlap values in both evaluated environments. Within riparian forests, the overlap coefficient reached 0.826, indicating strong coincidence between the activity patterns of both species. In this environment, both cervids exhibited records throughout the entire daily cycle, with coincident activity peaks around dusk and during the first nighttime hours (Figure 6). Activity of *A. axis* was characterized by broader temporal distribution, whereas *S. gouazoubira* tended to concentrate activity within crepuscular periods and part of the nighttime interval. Within native forests, the overlap coefficient was 0.785, also considered high, although lower than the value observed in riparian forests. In this case, a more differentiated pattern was observed: *S. gouazoubira* exhibited a predominantly crepuscular behavior, with activity peaks at dawn and dusk, whereas *A. axis* combined this pattern with a more pronounced increase in nocturnal activity. These findings suggest that although both species maintain substantial temporal overlap, the degree of coincidence is greater within riparian forests and comparatively reduced within native forests.

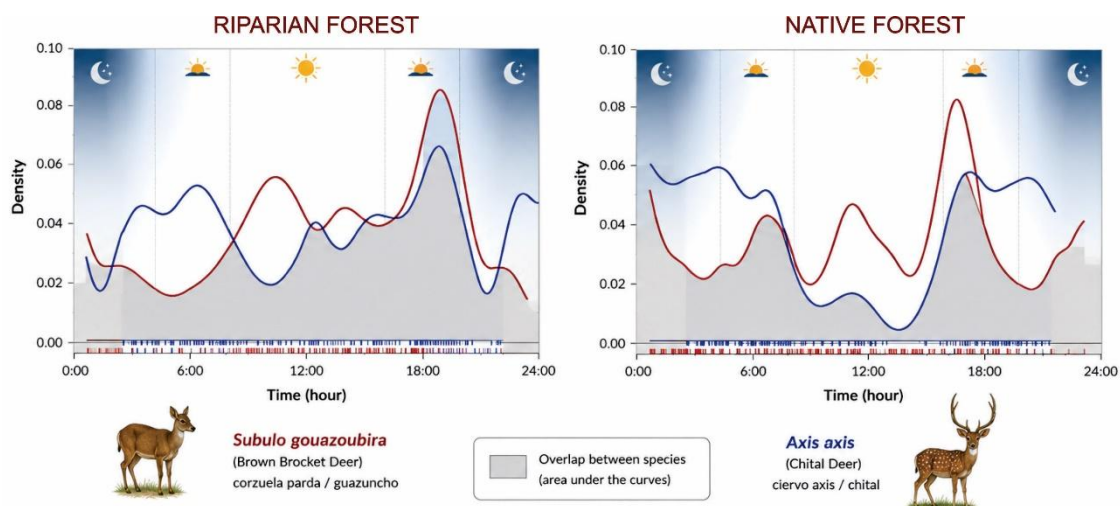


Figure 6. Temporal overlap of daily activity patterns between axis deer (*Axis axis*, blue line) and brown brocket deer (*Subulo gouazoubira*, red line) in two environments: riparian forest (left) and native forest (right). Curves represent probability density estimates derived from camera-trap records, whereas the gray shaded area indicates the temporal overlap between both species. Overlap coefficients were high in both environments ($\Delta = 0.826$ in riparian forest and $\Delta = 0.785$ in native forest).

Seasonal analyses of temporal overlap between *Subulo gouazoubira* and *Axis axis* within riparian forests revealed marked seasonal variation (Figure 7). During autumn, overlap was moderate ($\Delta = 0.54$), with brown brocket deer concentrating activity during dusk and early morning hours,

whereas axis deer exhibited a broader and more diffuse activity pattern throughout the day. During winter, the overlap index increased substantially ($\Delta = 0.82$), indicating strong coincidence between both species, with shared activity peaks during late afternoon and the first nighttime hours. In spring, the highest overlap value was recorded ($\Delta = 0.89$), with both cervids broadly coinciding in their crepuscular and nocturnal activity patterns. Finally, during summer, overlap remained high ($\Delta = 0.79$), with *S. gouazoubira* concentrating activity during early morning and dusk periods, whereas *A. axis* exhibited a broader temporal niche that also included diurnal activity.

In contrast, within native forests temporal overlap between both cervids varied considerably throughout the year. During autumn, overlap was moderate ($\Delta = 0.62$), with *S. gouazoubira* exhibiting a pronounced crepuscular pattern and *A. axis* extending activity into the early nighttime hours, resulting in only partial coincidence. During winter, the lowest overlap value was observed ($\Delta = 0.48$); brown brocket deer concentrated activity around dusk, whereas axis deer remained predominantly nocturnal, reducing temporal coincidence between species. In spring, overlap increased ($\Delta = 0.79$), with both species exhibiting coincident activity peaks during late afternoon and nighttime hours. Finally, during summer, overlap reached high values ($\Delta = 0.85$), with marked coincidence during early morning and dusk periods, when thermal conditions are comparatively more favorable.

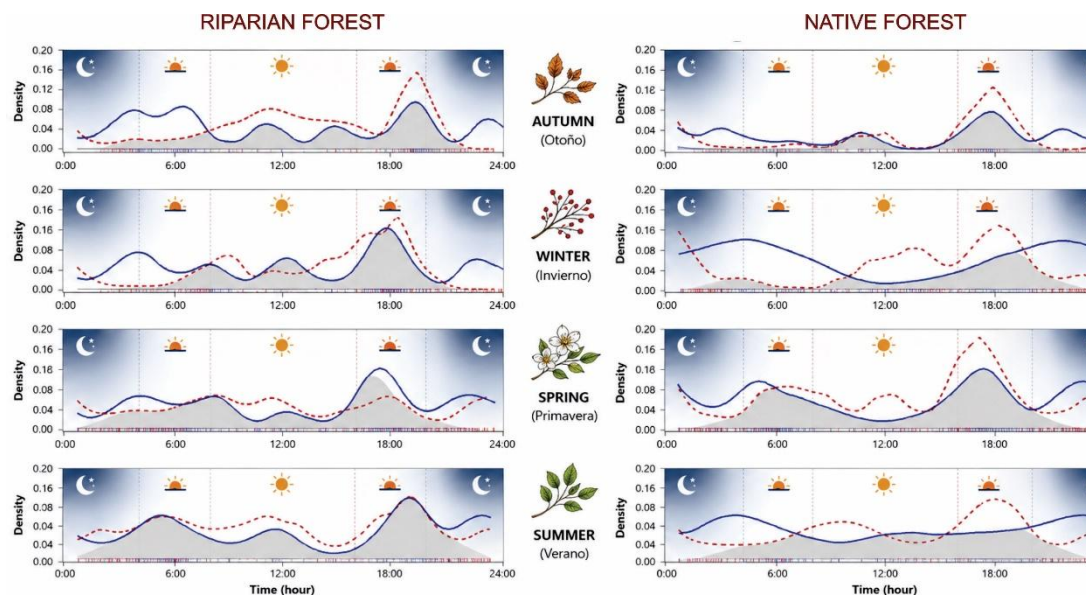


Figure 7. Seasonal temporal overlap of daily activity patterns between the cervids species present (*Axis axis* and *Subulo gouazoubira*) in two environments: riparian forest and native forest. Solid blue lines represent chital deer (*Axis axis*), whereas dashed red lines represent brown brocket deer (*Subulo gouazoubira*).

Comparisons between environments revealed contrasting patterns. Within riparian forests, temporal overlap remained consistently high throughout most of the year (winter: 0.82; spring: 0.89; summer: 0.79), reaching maximum values during spring and decreasing to moderate levels only during autumn (0.54). In contrast, within native forests temporal overlap exhibited greater variability, with lower values recorded during autumn (0.62) and particularly during winter (0.48), whereas during spring and summer overlap increased to high levels (0.79–0.85).

Population density estimates across environments

The analysis of monthly relative abundance revealed marked differences between *Axis axis* and *Subulo gouazoubira* across the two evaluated environments (Figure 8). Within riparian forests, axis deer consistently exhibited higher abundance values than brown brocket deer throughout most of the year, reaching a maximum peak in May ($\approx 5.7 \text{ ind}\cdot\text{ha}^{-1}$), with additional pronounced increases during August ($\approx 3.0 \text{ ind}\cdot\text{ha}^{-1}$) and November ($\approx 2.5 \text{ ind}\cdot\text{ha}^{-1}$). In contrast, *S. gouazoubira* maintained lower and comparatively more stable abundance values, with relatively higher densities recorded in January ($\approx 2.2 \text{ ind}\cdot\text{ha}^{-1}$) and December ($\approx 2.0 \text{ ind}\cdot\text{ha}^{-1}$), and minimum values during winter months (June–July, $<1.0 \text{ ind}\cdot\text{ha}^{-1}$). Within native forests, interspecific differences were less pronounced. Although axis deer maintained relatively high abundance values throughout the year, with peaks in November ($\approx 2.8 \text{ ind}\cdot\text{ha}^{-1}$), June ($\approx 1.8 \text{ ind}\cdot\text{ha}^{-1}$), and October ($\approx 1.9 \text{ ind}\cdot\text{ha}^{-1}$), the brown brocket deer reached similar or even higher values during winter. In particular, during July–August, *S. gouazoubira* exhibited its highest abundance estimates within this environment ($\approx 2.0\text{--}2.2 \text{ ind}\cdot\text{ha}^{-1}$), temporarily exceeding those recorded for axis deer. During the remainder of the year, abundance values remained lower ($<1.0 \text{ ind}\cdot\text{ha}^{-1}$), although the species maintained continuous presence throughout the annual cycle.

Overall, whereas axis deer dominated relative abundance almost permanently within riparian forests, the brown brocket deer retained greater seasonal importance within native forests, particularly during winter months.

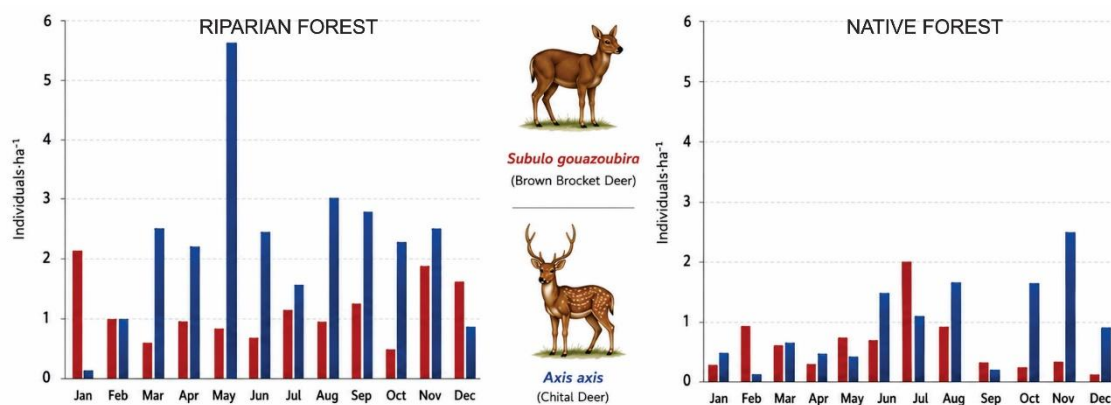


Figure 8. Monthly population density estimates of *Subulo gouazoubira* (brown brocket deer) and *Axis axis* (chital deer) in riparian forest and native forest environments of the Argentine Espinal. Values are expressed as individuals per hectare ($\text{ind}\cdot\text{ha}^{-1}$) based on camera-trap records and REST model estimations. Blue bars represent *Axis axis*, whereas red bars correspond to *Subulo gouazoubira*.

Discussion

Differences in abundance and habitat use

The results revealed marked differences in relative abundance and habitat use between the two cervid species evaluated. *Axis axis* exhibited the highest relative abundance values in both habitat types, particularly within riparian forests, where the greatest frequencies of records were observed. This trend confirms the high ecological plasticity of the species, which has been widely documented across different environments of the Argentine Mesopotamia and other South American regions (Pereira-Garbero et al., 2013; Tellarini et al., 2019; Shalom, 2023; Shalom et al., 2025). The ability of *Axis axis* to exploit both open sectors and environments with dense arboreal cover and permanent water availability may explain its success within heterogeneous and fragmented landscapes, especially in productive systems where forests, grasslands, and croplands coexist. In contrast, *Subulo gouazoubira* exhibited lower relative

abundance values and a more restricted distribution, mainly associated with riparian environments and sectors characterized by greater vegetation cover. The segregation observed between both species partially coincides with the findings of Juliá et al. (2019), who suggested that the expansion of axis deer may generate spatial displacement of native cervids through competition for habitat and resources. In the present study, although both species coexisted within the same environments and exhibited a high degree of syntopy, the brown brocket deer showed lower frequencies of occurrence in sites with high axis deer abundance, particularly within native forest sectors more intensively used by the exotic species. This pattern may indicate processes of partial exclusion or differential habitat use, in which the brown brocket deer occupies sectors subjected to lower competitive pressure or reduced anthropogenic disturbance. Nevertheless, the coexistence observed also supports the findings of Muzzachiodi et al. (2022), who described mixed groups and spatial overlap between both cervids within Espinal environments.

Interactions with cattle and horses may represent another important factor influencing the structure of these populations. Photographic records showed that *Axis axis* frequently shared the same sectors used by cattle, whereas *Subulo gouazoubira* increased its frequency of records after livestock removal from specific paddocks. These findings are consistent with those reported by Nanni (2015) and Di Bitetti et al. (2020), who documented a negative correlation between livestock presence and brown brocket deer activity, suggesting processes of spatial and temporal avoidance associated with competition for food resources, disturbance, or behavioral displacement. In this context, the greater tolerance of axis deer to livestock activity and anthropogenic disturbance may represent an additional ecological advantage over the native species. Overall, the results suggest that *Axis axis* behaves as a highly successful exotic species capable of exploiting a broad variety of habitats and disturbance conditions within productive systems of the Argentine Espinal. In contrast, *Subulo gouazoubira* appears to depend more strongly on environments characterized by greater vegetation complexity and lower disturbance levels. These differences may have important implications for the conservation of native cervids, particularly in landscapes where the expansion of axis deer and the intensification of productive activities continue to modify the structure and availability of natural habitats.

General activity patterns

The analysis of activity patterns indicated that both *Axis axis* and *Subulo gouazoubira* exhibited activity distributed throughout the entire daily cycle, being classified as cathemeral species according to the interval-based criteria proposed by Albanesi et al. (2016). Neither species concentrated more than 70% of its records within a single period of the day, nor reached 90% when combining crepuscular and nocturnal categories, confirming broad use of the 24-hour cycle. This behavior partially coincides with the findings of Beni et al. (2014), who described the brown brocket deer as a cathemeral species and axis deer as exhibiting predominantly crepuscular tendencies. Cathemerality has been defined as an activity strategy distributed across both light and dark periods throughout the 24-hour cycle (Tattersall, 2006; Tattersall, 2008), representing a flexible adaptation to environmental variability, resource availability, and disturbance pressure. However, continuous probability density analyses revealed important functional differences between both species that were not detected through discrete interval classifications. *Subulo gouazoubira* exhibited a predominantly crepuscular pattern, with activity peaks concentrated at dawn and particularly at dusk, whereas *Axis axis* displayed broader and more flexible activity, incorporating nocturnal periods and even diurnal activity in some environments. These differences were especially evident within riparian forests, where axis deer exhibited a more homogeneous and temporally extended activity distribution throughout the day. These findings are consistent with those reported by Pereira-Garbero et al. (2013) and Shalom et al. (2023), who described axis deer as a species with crepuscular-nocturnal behavior

and high temporal plasticity. The differences between both methodological approaches highlight the importance of applying continuous temporal analyses to interpret circadian patterns in wildlife species. Whereas interval-based classification confirmed the cathemeral condition of both cervids, Kernel Density and STN analyses revealed finer-scale differences in temporal activity organization, demonstrating greater crepuscular specialization in the brown brocket deer and greater temporal plasticity in *Axis axis*. These differences may reflect contrasting ecological strategies associated with habitat use and interspecific coexistence, where greater temporal flexibility could favor adaptation to disturbed environments and resource exploitation in invasive species.

Temporal strategies and ecological plasticity

The results revealed clear differences in the temporal strategies adopted by both species. *Subulo gouazoubira* maintained a predominantly crepuscular pattern in both environments, concentrating most of its activity during the first and last hours of the day. Within native forests, activity peaks were more clearly defined and consistent, especially during dusk, whereas within riparian forests activity was more diffuse and less intense. This behavior agrees with numerous studies conducted in Neotropical environments, where brown brocket deer exhibit predominantly crepuscular or diurnal-crepuscular tendencies associated with foraging strategies, thermal stress reduction, and decreased predation risk (Rivero et al., 2005; Pautasso et al., 2008; Albanesi et al., 2016; Grotta-Neto et al., 2024; Rodríguez et al., 2024). The greater temporal concentration observed within native forests further suggests that this environment may constitute higher-quality habitat or an area subjected to lower anthropogenic disturbance for the species. In contrast, *Axis axis* exhibited considerably greater temporal flexibility. Within native forests, activity was predominantly crepuscular-nocturnal, with marked increases during early morning hours and at dusk, whereas within riparian forests records were distributed more homogeneously throughout the entire daily cycle. These findings coincide with observations reported by Shalom et al. (2023, 2024) in El Palmar National Park and by Pereira-Garbero et al. (2013) in Uruguay, who described axis deer as a species with crepuscular and nocturnal habits, although highly variable according to environmental conditions. The temporal breadth observed in the present study reinforces the hypothesis that axis deer possess high behavioral plasticity, a common characteristic of successful invasive species capable of rapidly adjusting to heterogeneous and disturbed environmental conditions. Mean temperature likely constitutes one of the principal factors associated with these temporal variations. Several studies on ungulates have demonstrated that elevated temperatures reduce diurnal activity and promote shifts in foraging behavior toward nocturnal or crepuscular periods (du Toit and Yetman, 2005; Gallina and Bello Gutiérrez, 2014; Brivio et al., 2016). In the present study, both species markedly reduced activity during central daytime hours, particularly during summer, when temperatures are highest relative to annual averages. This pattern was especially evident within native forests, where activity curves exhibited pronounced declines around midday and increases during dawn and dusk. The use of thermally favorable periods may therefore represent a behavioral thermoregulation strategy aimed at reducing energetic expenditure and minimizing physiological stress.

In addition to thermal conditions, anthropogenic disturbance may also be modulating part of the observed activity patterns. In particular, the marked diurnal activity recorded for *Axis axis* within one riparian forest sector could be associated with greater arboreal cover, permanent water availability, and lower proximity to areas subjected to frequent movement of machinery, vehicles, and people. Within productive systems, ungulates commonly modify their activity schedules to minimize encounters with human disturbance (Di Bitetti et al., 2008; Wevers et al., 2020; Pardo et al., 2021; Passoni et al., 2021). In this context, the ability of axis deer to adjust activity according to local environmental conditions may represent an ecological advantage over

the brown brocket deer, whose activity remained more restricted and predictable across both environments.

Seasonal variation in activity patterns

Seasonal analyses revealed that both species modified their activity patterns throughout the year, adjusting the intensity and temporal distribution of records according to environmental conditions and habitat characteristics. In *Subulo gouazoubira*, the overall pattern remained predominantly crepuscular across all seasons, although changes were observed in the amplitude and timing of activity peaks. During autumn and spring, particularly within native forests, the species exhibited marked increases in activity at dusk, whereas during summer activity shifted toward early morning and dawn hours, accompanied by a substantial reduction in midday records. This behavior is consistent with observations reported for other Neotropical cervids, where seasonal variation in temperature and solar radiation directly influences foraging schedules and movement patterns (Rivero et al., 2005; Ferregueti et al., 2015; Grotta-Neto et al., 2024). During winter, both within riparian forests and native forests, the brown brocket deer exhibited broader temporal distribution and comparatively greater diurnal activity. This pattern may be associated with lower temperatures during this season, favoring increased activity during periods with more suitable thermal conditions. In temperate environments, several ungulate species increase activity during central daytime hours during colder periods in order to optimize energetic balance and reduce thermoregulatory costs (du Toit and Yetman, 2005; Gallina and Bello Gutiérrez, 2014). Furthermore, differences observed between environments suggest that riparian forests may provide more stable microclimatic conditions, allowing less temporally concentrated activity compared with native forests.

Axis axis also exhibited important seasonal variation, although maintaining broader temporal activity than *Subulo gouazoubira*. During autumn and winter, nocturnal and crepuscular activity predominated within native forests, whereas during spring and summer records were distributed more heterogeneously, including activity during morning hours and even around midday in some riparian forest sectors. These findings are consistent with those reported by Shalom et al. (2024), who observed seasonal shifts in axis deer activity patterns associated with thermal variation and vegetation cover availability. The greater temporal flexibility exhibited by axis deer may enable exploitation of a wider range of resources and habitats throughout the year, particularly within heterogeneous landscapes where water availability, shade, and food resources vary seasonally. Overall, the results suggest that seasonal variation in activity patterns is primarily associated with mechanisms of behavioral thermoregulation and differential habitat use. Both brown brocket deer and axis deer partially avoided periods of maximum temperature during summer by shifting activity toward cooler periods of the day, whereas during winter both species expanded their diurnal activity. Nevertheless, *Axis axis* exhibited considerably greater temporal flexibility, maintaining activity across a broader range of periods and environmental conditions. Such plasticity may represent an important adaptive advantage under scenarios of disturbance and environmental change within productive systems of the Argentine Espinal.

Temporal overlap and coexistence

Temporal overlap analyses revealed high coincidence in activity patterns between *Axis axis* and *Subulo gouazoubira* in both evaluated environments. The overlap coefficients obtained indicated high overlap within both riparian forests and native forests, suggesting that both species simultaneously exploit broad portions of the daily cycle. These findings reinforce the previously described syntopic condition of both cervids within Espinal and Argentine Mesopotamian environments (Muzzachiodi et al., 2022), demonstrating that both species are capable of coexisting spatially and temporally while sharing similar habitats. However, the

coexistence observed does not necessarily imply the absence of competition, but may instead reflect more complex mechanisms of resource partitioning and behavioral adjustment. Within riparian forests, temporal overlap remained consistently high throughout much of the year, reaching maximum values during winter and spring. In this environment, both species overlapped primarily during crepuscular periods and the first nighttime hours, although *Axis axis* exhibited broader and more extended temporal activity. The greater vegetation cover, permanent water availability, and reduced thermal amplitude characteristic of riparian forests may favor greater spatial and temporal coincidence between both species. Moreover, riparian forests constitute highly productive environments with abundant shelter availability, potentially reducing the intensity of direct competition and allowing more stable coexistence.

In contrast, native forests exhibited greater seasonal variability in overlap intensity, particularly during autumn and winter, when overlap values decreased substantially. During these seasons, *Subulo gouazoubira* maintained a predominantly crepuscular pattern, whereas *Axis axis* intensified nocturnal activity, partially reducing temporal coincidence between both species. This pattern may be interpreted as a form of partial temporal segregation, whereby differences in activity schedules contribute to reducing competition for resources or direct interspecific encounters. Temporal partitioning constitutes a widely documented mechanism within sympatric mammal communities, particularly in systems where ecologically similar species share habitat resources (Pianka, 1974; Di Bitetti et al., 2008). The broader temporal niche exhibited by *Axis axis* once again suggests elevated behavioral plasticity, enabling the species to adjust activity schedules according to environmental conditions, disturbance levels, and interactions with other species. In contrast, the brown brocket deer exhibited more restricted and predictable activity patterns, primarily associated with crepuscular periods. These differences may confer competitive advantages to axis deer within productive and disturbed environments, facilitating its expansion and persistence across heterogeneous Espinal landscapes. Nevertheless, the persistence of high overlap values in both environments also indicates that, under current conditions, both species maintain functional coexistence mechanisms allowing them to share resources and habitats within the studied system.

Ecological and management implications

The results obtained demonstrate that *Axis axis* is widely established within natural and productive environments of southern Argentine Mesopotamia, reaching high abundance levels and exhibiting remarkable spatial and temporal adaptability. The combination of ecological plasticity, broad temporal activity, and tolerance to environments characterized by livestock presence and anthropogenic disturbance likely explains the invasive success of the species within the Espinal region. Several studies have suggested that successful exotic species commonly exhibit high behavioral flexibility and the capacity to exploit resources across heterogeneous environments (Relva and Sanguinetti, 2016; Suarez Castro et al., 2021), characteristics that coincide with the patterns observed in the present study for axis deer.

In contrast, *Subulo gouazoubira* exhibited more restricted habitat use and more conservative temporal patterns, particularly associated with environments characterized by greater vegetation cover and lower disturbance levels. Although the species maintained spatial and temporal coexistence with axis deer, the observed differences in abundance and habitat use suggest that the brown brocket deer may be experiencing processes of partial displacement or reductions in available habitat quality. Simultaneous interactions with domestic livestock, productive activities, and exotic species may further intensify these limitations, particularly within fragmented landscapes or areas subjected to agricultural intensification. In this context, the conservation of heterogeneous environments containing native forest sectors and riparian forests becomes especially important for maintaining viable populations of native cervids within productive matrices.

These findings highlight the importance of continuing to investigate interactions among native cervids, exotic species, and agricultural activities within the Argentine Espinal. Understanding how these relationships vary across spatial and temporal scales will improve conservation and management strategies, particularly under ongoing processes of landscape transformation and invasive species expansion. Furthermore, the incorporation of long-term camera-trap monitoring programs may constitute a key tool for evaluating population changes, coexistence patterns, and behavioral responses under scenarios of environmental and productive change.

Conclusions

The results obtained allowed the characterization of ecological differences between *Axis axis* and *Subulo gouazoubira* within representative Espinal environments of southern Argentine Mesopotamia. Although both species were classified as cathemeral and exhibited high levels of temporal overlap, axis deer showed greater abundances, broader habitat use, and higher spatial and temporal plasticity, incorporating both diurnal and nocturnal activity according to environmental and seasonal conditions. In contrast, the brown brocket deer maintained activity patterns more strongly associated with environments characterized by greater vegetation cover and predominantly crepuscular behavior. Seasonal variation revealed adjustments in activity patterns associated with thermal conditions; however, *Axis axis* exhibited greater adaptive capacity, which may facilitate its expansion within productive and disturbed environments. Overall, the results suggest the existence of current functional coexistence between both species, although differences in abundance and habitat use may reflect early processes of competition or displacement associated with the expansion of the exotic species. Furthermore, this study highlights the usefulness of camera trapping and integrated temporal and population analyses as valuable tools for understanding the ecological dynamics of native and exotic ungulates, providing relevant information for wildlife conservation and management within Espinal ecosystems.

Acknowledgements

The authors thank the Protected Natural Area “La Esmeralda” for funding the study and granting permission to conduct fieldwork within the property. We also thank the Geoffroy’s Cat Working Group for providing financial and technical support during the execution of the study.

Ethics, Consent to Participate, and Consent to Publish declarations

Not applicable

Clinical trial number

Not applicable

References

- ✓ Albanesi SA, Jayat JP, Brown AD (2016) Patrones de actividad de mamíferos de medio y gran porte en el pedemonte de yungas del noroeste argentino. *Mastozoología neotropical*, 23(2): 335-358. https://mn.sarem.org.ar/wp-content/uploads/SAREM-SBMz_MastNeotrop_26-2_02_Albanesi.pdf

- ✓ APN (2019) Lineamientos técnicos para el ordenamiento y manejo ganadero en áreas protegidas de la Administración de Parques Nacionales. IF-2019-87633925-APN-DNC#APNAC. Administración de Parques Nacionales. Buenos Aires
- ✓ Arias A, Guzmán J (2023) Buenas prácticas para la coexistencia ganadería-fauna nativa. Boletín técnico de la Fundación Vida Silvestre Argentina, Buenos Aires. <https://www.vidasilvestre.org.ar/?25540/Buenas-practicas-para-la-coexistencia-Ganaderia-Fauna-Nativa---Boletin-tecnico-de-la-Fundacion-Vida-Silvestre-Argentina>
- ✓ Avogadro EG, Padró, JC (2019) Diferenciación de plantaciones forestales en Entre Ríos (Argentina): comparación de métodos de clasificación aplicados a imágenes Sentinel-2 y Landsat-8. *GeoFocus* 24: 117-139. <https://doi.org/10.21138/GF.652>
- ✓ Barzan FR (2023) Las aves como indicadoras de la degradación del bosque de Espinal con ganadería en Entre Ríos. Thesis submitted to qualify for the title of Doctor of the University of Buenos Aires in the area of Biological Sciences. Departamento de Ecología, Genética y Evolución. Facultad de Ciencias Exactas y Naturales. UBA, Buenos Aires. https://bibliotecadigital.exactas.uba.ar/download/tesis/tesis_n7513_Barzan.pdf
- ✓ Begon M, Harper JL, Townsend, CR (1986) *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications, Oxford
- ✓ Bennie JJ, Duffy JP, Inger R, Gaston KJ (2014) Biogeography of time partitioning in mammals. *Proc. Natl. Acad. Sci. U.S.A.* 111 (38) 13727-13732. <https://doi.org/10.1073/pnas.1216063110>
- ✓ Berduc A (2002) Plan de Manejo de la Reserva Natural Parque Enrique Berduc. Parque General San Martín. Consejo General de Educación, Entre Ríos.
- ✓ Blundell GM, Maier JA Debevec EM (2001) Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecological monographs*, 71(3): 469-489. [https://doi.org/10.1890/0012-9615\(2001\)071\[0469:LHREOS\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2001)071[0469:LHREOS]2.0.CO;2)
- ✓ Bohan D, et al (2017) Next-Generation Global Biomonitoring: Large-scale, Automated Reconstruction of Ecological Networks. *Trends in Ecology & Evolution* 32: 477-487. <http://dx.doi.org/10.1016/j.tree.2017.03.001>
- ✓ Botero AL, De La Ossa VJ (2011) Fauna silvestre asociada a ganado vacuno doble propósito en sistema de silvopastoreo, Pinto, Magdalena, Colombia. *Revista MVZ Córdoba* 16(3): 2733-2741. <https://doi.org/10.21897/rmvz.274>
- ✓ Brivio F, et al (2016). The weather dictates the rhythms: Alpine chamois activity is well adapted to ecological conditions. *Behav Ecol Sociobiol* 70, 1291–1304. <https://doi.org/10.1007/s00265-016-2137-8>
- ✓ Calfayan LM (2021) Comparación morfológica de heces de *Mazama gouazoubira* y del ciervo introducido *Axis axis* (Cetartiodactyla: Cervidae). *Notas Sobre Mamíferos Sudamericanos* 3(1). <https://doi.org/10.31687/saremNMS.21.7.2>
- ✓ Carthew SM, Slater E (1991) Monitoring animal activity with automated photography. *The Journal of Wildlife Management* 689-692
- ✓ Chandler RB, Royle JA (2013) Spatially explicit models for inference about density in unmarked or partially marked populations. *Ann. Appl. Stat.* 7(2): 936-954. <https://doi.org/10.1214/12-AOAS610>
- ✓ De Solla SR, Bonduriansky R, Brooks, RJ (1999) Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of animal ecology* 68(2): 221-234. <https://doi.org/10.1046/j.1365-2656.1999.00279.x>
- ✓ Di Bitetti MS, et al (2008) Differential responses to hunting in two sympatric species of brocket deer (*Mazama americana* and *M. nana*). *Biotropica* 40(5): 636-645. <https://doi.org/10.1111/j.1744-7429.2008.00413.x>
- ✓ Di Bitetti MS, et al (2020) Effects of cattle on habitat use and diel activity of large native herbivores in a South American rangeland. *Journal for Nature Conservation* 58, 125900. <https://doi.org/10.1016/j.jnc.2020.125900>

- ✓ Du Toit JT, CA Yetman (2005) Effects of body size on the diurnal activity budgets of African browsing ruminants. *Oecologia* 143:317–325. <https://doi.org/10.1007/s00442-004-1789-7>
- ✓ Eberhardt A, et al (2009) Distribución y conservación del Ciervo de los Pantanos (*Blastocerus dichotomus*) en la provincia de Santa Fe, Argentina. Resultados Preliminares. *Biológica* 10: 43-53
- ✓ Fedriani JM, et al. (2000) Competition and intraguild predation among three sympatric carnivores. *Oecologia* 125(2): 258-270. <https://doi.org/10.1007/s004420000448>
- ✓ Fernández-Durán JJ (2004) Circular distributions based on nonnegative trigonometric sums. *Biometrics* 60(2): 499-503. <https://doi.org/10.1111/j.0006-341X.2004.00195.x>
- ✓ Ferreguetti AC, Tomás WM, Bergallo HG (2015) Density, occupancy, and activity pattern of two sympatric deer (*Mazama*) in the Atlantic Forest, Brazil, *Journal of Mammalogy* 96(6): 1245–1254. <https://doi.org/10.1093/jmammal/gyv132>
- ✓ Gallina S, Bello Gutiérrez J (2014) Patrones de actividad del venado cola blanca en el noreste de México. *Therya* 5(2): 423–436. <https://therya.mastozoologiamexicana.com/index.php/THERYA/article/view/175>
- ✓ Gallina-Tessaro S, López-González C (2011) Manual de técnicas para el estudio de la fauna. Universidad Autónoma de Querétaro e Instituto de Ecología, AC México
- ✓ Gilbert NA, et al (2021), Abundance estimation of unmarked animals based on camera-trap data. *Conservation Biology* 35: 88-100. <https://doi.org/10.1111/cobi.13517>
- ✓ Gray TNE, et al (2018) The wildlife snaring crisis: an insidious and pervasive threat to biodiversity in Southeast Asia. *Biodiversity and Conservation* 27 (4): 1031-1037. <https://doi.org/10.1007/s10531-017-1450-5>
- ✓ Grotta-Neto F, et al (2024) Brouet deer niche breadth and overlap: spatial similarities limit species coexistence. *Journal of Zoology* 324 (1): 21-33. <https://doi.org/10.1111/jzo.13180>
- ✓ Gürtler RE, et al (2024) Taylor's law and quasi-experimental hunting of invasive wild boar and axis deer in a protected area of Northeastern Argentina. *Wildl Res* 51:WR23127. <https://doi.org/10.1071/WR23127>
- ✓ Hayashi K, Iijima H (2022) Density estimation of non-independent unmarked animals from camera traps. *Ecological Modelling* 472, 110100. <https://doi.org/10.1016/j.ecolmodel.2022.110100>
- ✓ Henrich M, et al (2022) Deer Behavior Affects Density Estimates With Camera Traps, but Is Outweighed by Spatial Variability. *Front. Ecol. Evol.* 10:881502. <https://doi.org/10.3389/fevo.2022.881502>
- ✓ Hongo S, et al (2021) A practical guide for estimating animal density using camera traps: Focus on the REST model. *bioRxiv*. <https://doi.org/10.1101/2021.05.18.444583>
- ✓ <https://doi.org/10.12933/therya-14-200>
- ✓ Jori F, et al (2021). Wildlife–livestock interactions in animal production systems: what are the biosecurity and health implications?. *Animal Frontiers*, 11(5): 8-19. <https://doi.org/10.1093/af/vfab045>
- ✓ Jozami JM, Muñoz JDD (1982) Árboles y arbustos indígenas de la provincia de Entre Ríos. IPNAYS (CONICET-UNL)
- ✓ Juliá JP, et al (2019). *Mazama gouazoubira*. En: SAYDS–SAREM (eds.) Categorización 2019 de los mamíferos de Argentina según su riesgo de extinción. Lista Roja de los mamíferos de Argentina. <https://cma.sarem.org.ar/es/especie-nativa/mazama-gouazoubira>
- ✓ Karanth KU, Nichols JD (eds.) (2002). Monitoring tigers and their prey, a manual for researchers, managers and conservationist in tropical Asia. Centre for Wildlife Studies. Bangalore, India.
- ✓ Li X, et al (2022) CameratrappR: An R package for estimating animal density using camera trapping data. <https://doi.org/10.1016/j.ecoinf.2022.101597>
- ✓ Linkie M, Ridout MS (2011) Assessing tiger–prey interactions in Sumatran rainforests. *Journal of Zoology*, 284(3): 224-229. <https://doi.org/10.1198/jabes.2009.08038>

- ✓ Lyet A, et al (2024), Estimating animal density using the Space-to-Event model and bootstrap resampling with motion-triggered camera-trap data. *Remote Sens Ecol Conserv*, 10: 141-155. <https://doi.org/10.1002/rse2.361>
- ✓ Lynam AJ, et al (2013) Terrestrial activity patterns of wild cats from camera-trapping. *Raffles Bulletin of Zoology* 61(1). <https://www.science.nus.edu.sg/wp-content/uploads/sites/11/2013/08/61rbz407-415.pdf>
- ✓ Maldonado FD, Fernando Tentor F, Sione W (2012) Extensión de la faja Gauss-Krüger para el mapeo operacional de la provincia de Entre Ríos Paper presented at XXVI jornadas forestales de Entre Ríos, EEA INTA Concordia, Octubre de 2012. https://www.jornadasforestales.com.ar/jornadas/2012/trab_res_pos/534.9.TE.Maldonado.pdf
- ✓ Mandujano S (2019) Índice de Abundancia Relativa: RAI. In: Mandujano Rodríguez, S, Pérez Solano LA (Eds.) *Fototrampeo en R: Organización y Análisis de Datos Volumen 1*. Instituto de Ecología. Veracruz, México, p 137–152
- ✓ McIntyre T, et al (2020) Quantifying imperfect camera-trap detection probabilities: implications for density modelling. *Wildlife Research* 47, 177-185. <https://doi.org/10.1071/WR19040>
- ✓ Meredith M, Ridout MS (2020) Estimates of Coefficient of Overlapping for Animal Activity Patterns. The overlap package. Version 0.3.3 <https://github.com/mikemeredith/overlap/issue>
- ✓ Monroy-Vilchis O, et al (2011) Fototrampeo de mamíferos en la Sierra Nanchititla, México: abundancia relativa y patrón de actividad. *Revista de Biología Tropical* 59(1): 373-383
- ✓ Monterroso P, Alves PC, Ferreras P (2014) Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence. *Behav Ecol Sociobiol* 68, 1403–1417. <https://doi.org/10.1007/s00265-014-1748-1>
- ✓ Muñoz J, Milera S, Romero C, Brizuela A (2005) Bosques nativos y selvas ribereñas en la Provincia de Entre Ríos. *INSUGEO Miscelánea* 14: 169-182. <https://www.insugeo.org.ar/publicaciones/docs/misc-14-15.pdf>
- ✓ Muzzachiodi N, et al (2020) Puma concolor (Linnaeus, 1771) en la provincia de Entre Ríos: modelando su distribución actual y las áreas prioritarias para su conservación. *Historia Natural* 10(3): 157-178. https://fundacionazara.org.ar/img/revista-historia-natural/tercera-serie-volumen-10-3-2020/HN%2010_3%20Articulo%2012_157-178.pdf
- ✓ Muzzachiodi N, Sabattini JA (2025) Ritmos circadianos de los armadillos *Dasypus novemcinctus* y *Euphractus sexcinctus* en el Área Natural Protegida «La Esmeralda», Espinal entrerriano, República Argentina. *Notas Sobre Mamíferos Sudamericanos*, 7(1). <https://doi.org/10.31687/SaremNMS25.1154>
- ✓ Muzzachiodi N, Sabattini JA, Sabattini RA (2022) El guazuncho entrerriano (*Mazama gouazoubira* Fischer, 1814): historia natural, distribución y conservación. *Historia Natural Tercera Serie Volumen 12 (2)*: 137-163. https://fundacionazara.org.ar/img/revista-historia-natural/tercera-serie-volumen-12-2-2022/HN_12_2_137-163.pdf
- ✓ Nakashima Y, Hongo S, Akomo-Okoue EF (2020) Landscape- scale estimation of forest ungulate density and biomass using camera traps: Applying the REST model. *Biological Conservation*, 241,108381. <https://doi.org/10.1016/j.biocon.2019.108381>
- ✓ Nakashima Y, Yajima G, Hongo S (2021) Estimating animal density with camera traps: a practitioner's guide of the REST model. *bioRxiv*, 2021-05. <https://doi.org/10.1101/2021.05.18.444583>
- ✓ Nakashima Y, Yajima G, Matsuoka R (2025) ctrest: R package for density estimation using the REST and the RAD-REST model (v1.0). [Software]. Zenodo. <https://zenodo.org/records/17972657>
- ✓ Nakashima Y, Yajima G, Matsuoka R (2026). Reducing data processing effort in camera trap density estimation: Extending the REST model by explicitly modelling animal detection

processes. *Methods in Ecology and Evolution*, 17, 850–862. <https://doi.org/10.1111/2041-210x.70248>

- ✓ Nanni AS (2015) Dissimilar responses of the Gray brocket deer (*Mazama gouazoubira*), Crab-eating fox (*Cerdocyon thous*) and Pampas fox (*Lycalopex gymnocercus*) to livestock frequency in subtropical forests of NW Argentina. *Mammalian Biology* 80(4): 260–264. <https://doi.org/10.1016/j.mambio.2015.04.003>
- ✓ Navas J (1987) Los vertebrados exóticos introducidos en la Argentina *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Zoología* 14:7–38. <https://naturalis.fcnym.unlp.edu.ar/bitstreams/572143af-4192-4103-8f97-8155b30bf571/download>
- ✓ Nichols JD (1992) Capture-recapture models: using marked animals to study population dynamics. *Bioscience* 42: 94–102. <https://doi.org/10.2307/1311650>
- ✓ O'Brien TG (2011) Abundance, density and relative abundance: A conceptual framework. In: O'Connell AF, Nichols JD, Karanth KU (Edts). *Camera traps in animal ecology: methods and analyses*. Springer, Tokyo
- ✓ O'Connell Jr AF, et al (2006). Estimating site occupancy and detection probability parameters for meso-and large mammals in a coastal ecosystem. *The Journal of Wildlife Management* 70(6): 1625–1633. [https://doi.org/10.2193/0022-541X\(2006\)70\[1625:ESOADP\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2006)70[1625:ESOADP]2.0.CO;2)
- ✓ O'Connell Jr AF, Nichols JD, Karanth KU (Eds) (2011) *Camera traps in animal ecology: methods and analyses*. Springer, New York
- ✓ Ofstad EG, et al (2016) Home ranges, habitat and body mass: simple correlates of home range size in ungulates. *Proc. R. Soc. B* 283: 20161234. <http://dx.doi.org/10.1098/rspb.2016.1234>
- ✓ Oyarzabal M, et al (2018) Unidades de vegetación de la Argentina. *Ecología Austral* 28(1): 040–063. <https://doi.org/10.25260/EA.18.28.1.0.399>
- ✓ Palencia P, et al (2021) Assessing the camera trap methodologies used to estimate density of unmarked populations. *J Appl Ecol.* 58: 1583–1592. <https://doi.org/10.1111/1365-2664.13913>
- ✓ Palencia P, et al (2022). Random encounter model is a reliable method for estimating population density of multiple species using camera traps. *Remote Sensing in Ecology and Conservation* 8 (5): 670–682. <https://doi.org/10.1002/rse2.269>
- ✓ Palencia P, et al (2023). Inter-population variability in movement parameters: practical implications for population density estimation. *Journal of Wildlife Management* 87:e22473. <https://doi.org/10.1002/jwmg.22473>
- ✓ Pardo LE, et al (2021) Effects of oil palm and human presence on activity patterns of terrestrial mammals in the Colombian Llanos. *Mammalian Biology* 101: 775–789. <https://doi.org/10.1007/s42991-021-00153-y>
- ✓ Passoni G, et al. (2021) Roads constrain movement across behavioural processes in a partially migratory ungulate. *Mov Ecol* 9, 57. <https://doi.org/10.1186/s40462-021-00292-4>
- ✓ Pastore M (2018) Overlapping: a R package for estimating overlapping in empirical distributions. *Journal of Open Source Software* 3(32), 1023. <https://joss.theoj.org/papers/10.21105/joss.01023>
- ✓ Pautasso AA. (2008) Mamíferos de la provincia de Santa Fe, Argentina. *Comunicaciones del Museo Provincial de Ciencias Naturales Florentino Ameghino (Nueva Serie)* 13:1–248.
- ✓ Paviolo A, et al (2009) Protection affects the abundance and activity patterns of pumas in the Atlantic Forest. *Journal of Mammalogy* 90(4): 926–934. <https://doi.org/10.1644/08-MAMM-A-128.1>
- ✓ Peral C, Landman M, Kerley GI (2022). The inappropriate use of time-to-independence biases estimates of activity patterns of free-ranging mammals derived from camera traps. *Ecology and Evolution*, 12(10), e9408. <https://doi.org/10.1002/ece3.9408>

- ✓ Pereira-Garbero R, et al (2013) Mamíferos invasores en Uruguay, historia, perspectivas y consecuencias. Revista chilena de historia natural, 86(4): 403-421. <https://www.scielo.cl/pdf/rchnat/v86n4/art03.pdf>
- ✓ Pérez-Irineo G, Santos-Moreno ASM (2012) Diversidad de mamíferos terrestres de talla grande y media de una selva subcaducifolia del noreste de Oaxaca, México. Revista Mexicana de Biodiversidad 83(1): 64-169. <https://doi.org/10.22201/ib.20078706e.2012.1.792>
- ✓ Periago M (2006) Estimación de la densidad poblacional de la corzuela parda (*Mazama gouazoubira*) en la Reserva Chancaní (Córdoba, Argentina): puesta a punto de una técnica de muestreo. Thesis submitted to qualify for the title of Master, Programa de Posgrado en Manejo de Vida Silvestre Facultad de Ciencias Exactas, Físicas y Naturales. UNC, Córdoba
- ✓ Pianka ER (1974) Niche Overlap and Diffuse Competition. Proceedings of the National Academy of Sciences of the United States of America 71: 2141–2145. <https://doi.org/10.1073/pnas.71.5.2141>
- ✓ Pianka ER (2000) Evolutionary Ecology. Sixth Edition. Benjamin-Cummings, San Francisco
- ✓ Pratas-Santiago LP, et al (2016) The moon cycle effect on the activity patterns of ocelots and their prey. Journal of Zoology 299(4): 275-283. <https://doi.org/10.1111/jzo.12359>
- ✓ R Core Team (2013) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org/>
- ✓ Rebollo S, Gómez-Sal A (2003). Aprovechamiento sostenible de los pastizales. Ecosistemas 12 (3): 1-10. <https://revistaecosistemas.net/index.php/ecosistemas/article/view/231>
- ✓ Relva MA, Sanguinetti J (2016) Ecología, impacto y manejo del ciervo colorado (*Cervus elaphus*) en el Noroeste de la Patagonia, Argentina. Mastozoología Neotropical 23(2): 221-238. https://mn.sarem.org.ar/wp-content/uploads/SAREM-SBMz_MastNeotrop_23-2_03_El-Relva.pdf
- ✓ Ridout MS, Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. JABES 14, 322–337. <https://doi.org/10.1198/jabes.2009.08038>
- ✓ Rivero K, Rumiz DI, Taber AB (2005) Differential habitat use by two sympatric brocket deer species (*Mazama americana* and *M. gouazoubira*) in a seasonal Chiquitano forest of Bolivia. Mammalia 69(2): 169-183. <https://www.degruyterbrill.com/document/doi/10.1515/mamm.2005.015/html>
- ✓ Rodríguez D, et al (2024). Following the trail of the grey brocket deer (*Mazama gouazoubira*) in Argentina: new locality records, activity patterns and habitat use. THERYA, 15(1), 17–27. <https://therya.mastozoologiamexicana.com/index.php/THERYA/article/view/6120>
- ✓ Rojido IJ, Canavelli SB, Anderson CB (Eds) (2022) El espinal entrerriano: una perspectiva integral para su cuidado. Ediciones INTA, Estación Experimental Agropecuaria Paraná. <https://repositorio7.inta.gob.ar/bitstreams/b68342e8-6ccd-4cba-841d-d1a539bbee08/download>
- ✓ Sabattini J A, Sabattini R A (2021) Rainfall Trends in Humid Temperate Climate in South America: Possible Effects in Ecosystems of Espinal Ecoregion. Global Warming and Climate Change. IntechOpen. doi: 10.5772/intechopen.9908
- ✓ Sabattini JA, Sabattini RA, Ledesma S (2015). Caracterización del bosque nativo del centro norte de Entre Ríos (Argentina). Agrociencia Uruguay 19(2): 8-16. <https://doi.org/10.31285/AGRO.19.296>
- ✓ Sabattini JA, Sabattini RA, Muzzachiodi N, Treisse I, Penco R (2024) Mapping of the natural and anthropic environments of Entre Rios (Argentina) using machine learning classification. Revista de Teledetección 64: 49-60. <https://doi.org/10.4995/raet.2024.20831>
- ✓ Sabattini RA, et al (1999) Guía para la caracterización de agroecosistemas del centro-norte de Entre Ríos. Revista Científica Agropecuaria 3: 7 – 19
- ✓ Sasal MC, et al (2019) Capítulo Provincia de Entre Ríos. In: RR Casas, F Damiano (Eds). Manual de Buenas Prácticas de Conservación del Suelo y del Agua en Áreas de Secano. PROSA – FECIC, Buenos Aires

- ✓ Shalom I (2023) Distribución espacial y horarios de actividad de la fauna nativa y exótica de mediano y gran tamaño en el Parque Nacional El Palmar, Entre Ríos, Argentina. Thesis to opt for the degree of Bachelor in Biological Sciences. Departamento de Ecología, Genética y Evolución. Facultad de Ciencias Exactas y Naturales. UBA, Buenos Aires.
- ✓ Shalom I, et al (2025) Do exotic invasive mammals disturb the native fauna? Spatiotemporal distribution and overlap between species in a national park of Argentina. *Integrative Zoology* 20: 344–360. <https://doi.org/10.1111/1749-4877.12848>
- ✓ Solís Neffa VG, et al (2021) Identificación de vacíos ecorregionales. Informe Final para la Administración de Parques Nacionales (Proyecto GEF TF OA0233). APN, Buenos Aires. https://sib.gob.ar/archivos/vacios_conservacion_ecorregionales_GEF_APN.pdf
- ✓ Suárez-Castro AF, et al (2021). Vacíos de información espacial sobre la riqueza de mamíferos terrestres continentales de Colombia. *Caldasia* 43(2), 247-260. <https://doi.org/10.15446/caldasia.v43n2.85443>
- ✓ Tattersall I (2006) The concept of cathemerality: history and definition. *Folia Primatologica* 77: 7 – 14. <https://doi.org/10.1159/000089692>
- ✓ Tattersall I (2008) Avoiding commitment: Cathemerality among primates. *Biological Rhythm Research* 39: 213-228. <https://doi.org/10.1080/09291010701683292>
- ✓ Tellarini JF, et al (2019) Axis axis. In: SAYDS–SAREM (eds.) Categorización 2019 de los mamíferos de Argentina según su riesgo de extinción. Lista Roja de los mamíferos de Argentina. <https://cma.sarem.org.ar/es/especie-exotica/axis-axis>
- ✓ Tellarini JF, Merino ML, Pereira JA (2023) Axis axis, chital, ciervo axis. In: Valenzuela A, et al. *Introduced Invasive Mammals of Argentina. Mammalogical Research Volume 3*. SAREM, Mendoza, pp 215–221. <https://www.sarem.org.ar/wp-content/uploads/2021/04/SAREM-Axis-axis-Introduced-Invasive-Mammals-of-Argentina-2023.pdf>
- ✓ Tobler MW (2008) The ecology of the Lowland Tapir in Madre de Dios, Peru: using new technologies to study large rainforest mammals. Ph.D. thesis, Texas A&M University, College Station, Texas, USA.
- ✓ Tobler MW, Carrillo-Percegue SE, Powell G (2009) Habitat use, activity patterns and use of mineral licks by five species of ungulate in south-eastern Peru. *Journal of Tropical Ecology* 25(3): 261-270. doi:10.1017/S0266467409005896
- ✓ Trolliet F, et al (2014) Use of camera traps for wildlife studies. A Review. *Biotechnol. Agron. Soc. Environ.* 18(3): 446-454. <https://wolf.org/wp-content/uploads/2023/07/Trolliet-et-al-2014.pdf>
- ✓ Valenzuela A, et al (2023) *Introduced Invasive Mammals of Argentina*. Sociedad Argentina para Estudio de los Mamíferos SAREM, Mendoza
- ✓ Vantarová KH, et al (2023). Biological invasions in the twenty-first century: a global risk. *Biologia* 78(5), 1211-1218. <https://doi.org/10.1007/s11756-023-01394-7>
- ✓ Vilá B (2016) Camélidos sudamericanos. Colección Ciencia Joven 40. Eudeba, Buenos Aires
- ✓ Wevers J (2020) Trading fear for food in the Anthropocene: How ungulates cope with human disturbance in a multi-use, suburban ecosystem. *Science of The Total Environment* 741,140369. <https://doi.org/10.1016/j.scitotenv.2020.140369>
- ✓ Zampetti, A, et al (2024) Towards an automated protocol for wildlife density estimation using camera-traps. *Methods in Ecology and Evolution* 15: 2276–2288. <https://doi.org/10.1111/2041-210X.14450>